

# Human vision fails to distinguish widespread sexual dichromatism among sexually "monochromatic" birds

Muir D. Eaton\*

Bell Museum of Natural History, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108

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Historical scenarios of evolution of avian plumage coloration have been called into question with the discoveries that most birds can see UV light (which normal humans cannot), and that UV-reflecting plumages are widespread in birds. Several examples of sexual dichromatism not detectable with human visual capabilities suggest that our categorizations of plumages as sexually mono- or dichromatic might often be incorrect. Nonetheless, given the limited taxonomic scope of those examples, the vast majority of sexually monochromatic birds are still treated as such without question in avian research. Herein, I show that >90% of 139 species, in a broad sampling of presumed sexually monochromatic passerine birds, were actually sexually dichromatic from an avian visual perspective, based on comparisons of plumage reflectance data using a visual model of color discrimination thresholds. The taxonomic ubiquity of this result suggests that many existing interpretations of evolutionary patterns of sexual dichromatism in birds are erroneous. The visual model used herein provides a method for quantifying sexual dichromatism, revealing that most (58.7%) feather patches sampled lie along a continuum of dichromatism between avian and human discriminatory abilities and could represent unrecognized sexually selected signals. Sexual dichromatism in this study rarely resulted from intersexual differences in UV coloration *alone*, emphasizing the need for analysis of bird coloration in relation to the full extent of avian visual discriminatory abilities, including, but not limited to, UV-visual capabilities.

color vision | plumage evolution

Since Darwin, explaining the function and evolution of morphological differences between males and females (sexual dimorphism) has generated intense scientific interest (1). Birds exhibit impressive examples of sexual dimorphism, often due to striking differences in plumage coloration between males and females (i.e., sexual dichromatism). Sexually dichromatic species are often assumed to have evolved from sexually monochromatic ancestors, by means of sexual selection for trait elaboration (2). However, existing interpretations of evolution of sexual dichromatism are based on human visual assessments of avian coloration (e.g., 3–5). The validity of this approach has been questioned in recent decades, with the demonstration that many bird species can see UV wavelengths due to the presence of a fourth cone cell type in the retina that is receptive to UV light (6, 7). Avian color discrimination is also fundamentally different from that of humans: Birds perceive a greater diversity of colors than do humans (8) and are capable of differentiating two colors within human color space that humans cannot discriminate, because of oil droplets associated with each type of photoreceptive cone cell (9, 10).

More recent discoveries of examples of sexual dichromatism hidden from human perception (11–16) further suggest that previous interpretations of avian plumage coloration may be misleading (13). Specifically, large numbers of species appearing sexually monochromatic to humans (henceforth monochromatic<sup>human</sup>) may in fact be perceived as sexually dichromatic by birds (henceforth

dichromatic<sup>avian</sup>). Although existing research showing hidden coloration in avian plumage has focused on UV wavelengths (e.g., refs. 11, 12, and 17), evidence exists that differences in plumage colors extend across the portion of the light spectrum perceptible to humans (15, 16, 18). Hence, analyses of avian coloration should consider the full extent of avian visual capabilities to assess avian sexual dichromatism across species (13). Herein, I analyze the plumage coloration of 139 monochromatic<sup>human</sup> passerine species using a visual model of color discrimination (19) and demonstrate that interpretations of avian coloration based on human visual capabilities are almost invariably erroneous.

## Materials and Methods

**Data Collection.** I sampled all color patches on 139 sexually monochromatic<sup>human</sup> species from the order Passeriformes (see Table 1, which is published as supporting information on the PNAS web site), 49 of which had previously been identified as monochromatic, and the remaining 90 identified by me in review of specimen series. Two species were chosen from every subfamily [in Fringillinae two species were chosen from every tribe (20)]. All species chosen by me were confirmed as monochromatic<sup>human</sup> by two independent observers unaware of the project goals. For each species, I selected research study skins of five males and five females with the freshest-looking breeding-season plumage from the same general locality when possible. All specimens examined were from the collections at the Field Museum of Natural History and the American Museum of Natural History.

I sampled colors using an Ocean Optics (Dunedin, FL) S2000 spectrometer equipped with an R200–7-UV/VIS reflectance probe and a PX-2 pulsed xenon light source. Data, which consist of the percentage of light reflected at each wavelength from 300 to 700 nm calibrated against a Spectralon white reflectance standard, were collected with OOIBASE32 software (10 scans averaged per reading), with the reflectance probe oriented perpendicular to the measured surface. The probe was housed in a black rubber hose to minimize incident light and keep the measurement distance constant.

Color measurements were taken within "feather patches," defined as areas of continuous human-visual coloration (e.g., black, blue, and yellow) >4 mm<sup>2</sup> (the limit of resolution for the equipment). Therefore, finely barred, streaked, or mottled plumage was ignored. Depending on species' coloration patterns, I sampled one to eight patches per species, for a total of 552 feather patches sampled among the 139 study species, with 10 measurements (5 male and 5 female) saved for each patch. Raw spectral data were averaged into 10-nm bins between 300 and

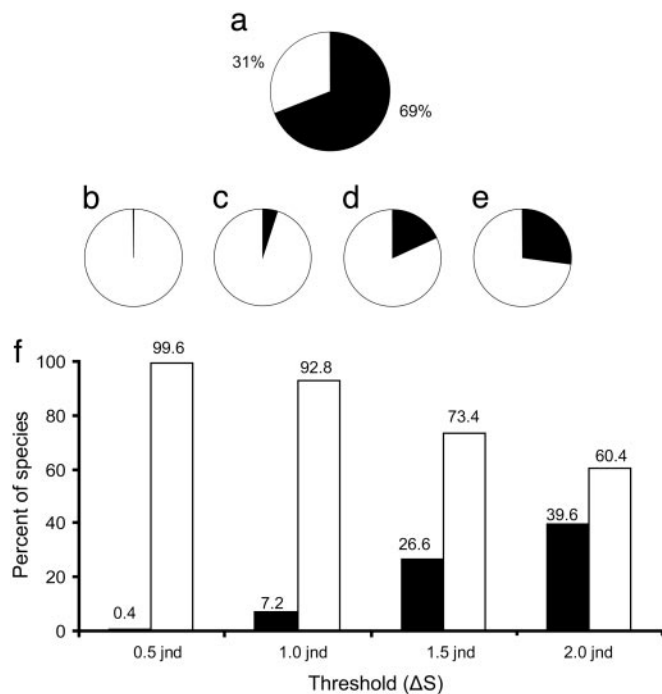
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Abbreviation: jnd, just noticeable differences.

\*Present address: Natural History Museum and Biodiversity Research Center, University of Kansas, Dyche Hall, 1345 Jayhawk Boulevard, Lawrence, KS 66045-7561. E-mail: muir@ku.edu.

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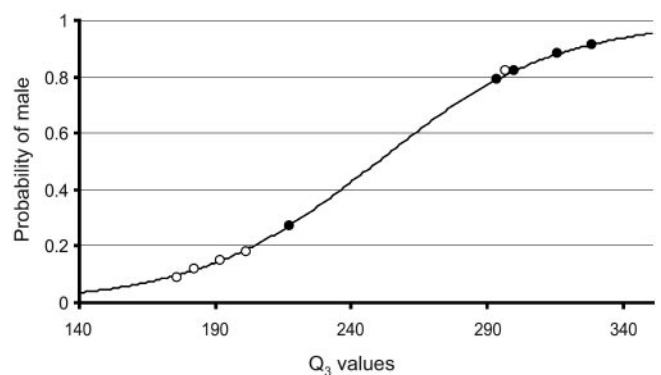




**Fig. 1.** Percent of passerine species classified as sexually monochromatic (black) or sexually dichromatic (white). (a) Estimated proportions of all passerines (by 30) based on human visual capabilities. (b–e) Reestimated proportions of all passerines from an avian visual perspective, based on the results of this study. (f) Percent of 139 human perceived sexually monochromatic species sampled defined as sexually monochromatic or sexually dichromatic under the Vorobyev–Osorio model (19), assuming different discrimination thresholds of  $\Delta S$  (in jnd). Each reestimation (b–e) is derived from the corresponding (directly below) percentage of dichromatic species shown in f, based on the indicated discrimination threshold value. The plumage classifications of the majority of all passerine species are in conflict from an avian visual perspective compared with a human visual perspective (compare a with b–e), unless threshold discrimination was set very conservatively ( $\geq 2.0$  jnd).

( $\Delta S = 2.0$  jnd), 84 of 139 (60.4%) species were dichromatic<sup>avian</sup> (Fig. 1f). Passerine birds represent the largest avian radiation [ $>5,000$  species (20)], and previous workers have estimated that 69% of these species are sexually monochromatic<sup>human</sup> (30) (Fig. 1a). Whereas some have pointed out that this estimate may be slightly high (13), my results indicate that it is a *vast* overestimate when avian visual capabilities are considered. Even under conservative thresholds for discrimination (1.5–2.0 jnd), I reestimated that only 18.4–27.3% of all passerines are sexually monochromatic<sup>avian</sup> (Fig. 1d and e). Historical dependence on human color perception has led to overestimates of numbers of species that are functionally monochromatic (i.e., monochromatic<sup>avian</sup>); my results revealed widespread conflict between human and avian perception of plumage for a large proportion of these species (Fig. 1b–e).

The human-avian perceptual conflict of plumage for many birds calls into question current interpretations of evolutionary patterns of sexual dichromatism. Mistaken designation of a large proportion of dichromatic<sup>avian</sup> species as monochromatic focused research on evolution of sexual dichromatism to a state detectable with human visual capabilities, consequently interpreting gains of sexual dichromatism as the origins of sexual dichromatism. Furthermore, although dichromatic forms have often been assumed to be derived from monochromatic forms by means of sexual selection for ornamentation (2), recent research has found sexual dichromatism commonly to be the ancestral condition, with selection acting to reduce ornamentation in one



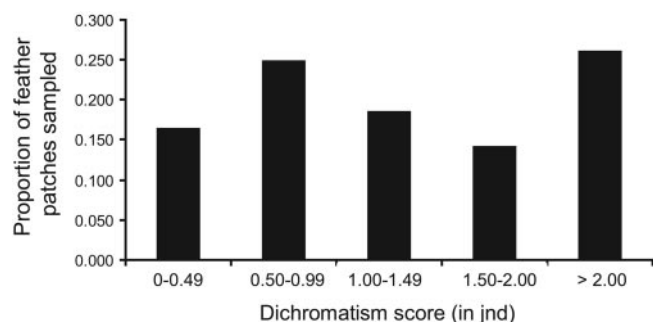
**Fig. 2.** Example of one quantum catch ( $Q_i$ ) that was strongly correlated with sex under a logistic regression model. The example shown here, from the head coloration of *Prinia atrogularis*, used a logit link function to back transform the predicted probability of an individual being male given a value for  $Q_3$  (i.e., quantum catch for the middle-wave sensitive cone; Eq. 1), based on the regression coefficient estimate (Table 1) from logistic regression modeling (see *Materials and Methods*). The five male  $Q_3$  (black circles) and five female  $Q_3$  (white circles) values used to estimate the regression coefficient are plotted to confirm that increasing values of  $Q_3$  strongly correlate with an increasing probability of an individual being male in this example.

sex (reviewed in ref. 5). The prevalence of dichromatic<sup>avian</sup> species found in this study, including several basal passerine lineages (31), suggests that comparative methods would reconstruct a dichromatic<sup>avian</sup> ancestor for all passerines, although detailed analyses remain to be conducted. In general, my results support a revised picture: A few monochromatic forms evolved from dichromatic forms, although an extreme bias in the evolution of dichromatism from monochromatic<sup>avian</sup> ancestors cannot be ruled out (32). Ultimately, further targeted taxon sampling combining analyses of plumage coloration relevant to avian visual capabilities with comparative methods is needed to determine the directionality of plumage change within passerine lineages.

The Vorobyev–Osorio model defines color discrimination based on integration across the entire range of visual wavelengths, giving no indication as to the relative contributions of specific wavelengths causing perceptual differences. UV plumage colors have been shown recently to be taxonomically widespread in birds (18, 33, 34), contributing to sexual dichromatism that humans cannot see (11–16). However, logistic regression modeling showed that only 23 of 552 (4.2%) feather patches sampled (representing 22 species) had strong correlations between *only*  $Q_1$  (i.e., the UV quantum catch) and sex (see Table 1). In contrast, 198 of 552 (35.9%) feather patches had strong correlations between at least one of  $Q_2$ – $Q_4$  and sex, indicating that wavelengths within the human visual range (400–700 nm) were strong predictors of sex, even though a given pair of homologous feather patches appeared as identical to the human eye. Hence, sexual dichromatism hidden from human perception commonly spans wavelengths within human visual capabilities ( $Q_2$ – $Q_4$ ), and not just in the UV. My data suggest that future studies need to consider the potential for intersexual color differences perceptible to the avian visual system even on species lacking plumage with likely UV-reflecting colors (e.g., blue or violet; see refs. 15, 16, and 18).

For 119 of 139 (85.6%) species sampled, at least one quantum catch for one feather patch was strongly correlated with sex (Fig. 2). For 33 of 552 (6.0%) feather patches (found on 28 species) there was no overlap in quantum catch values between males and females for at least one  $Q_i$ , and thus that portion of coloration predicted sex perfectly (see Table 1). My results are based on relatively small sample sizes for each





**Fig. 3.** Proportions of 552 feather patches sampled from 139 human-perceived sexually monochromatic species with different magnitudes of sexual dichromatism from an avian visual perspective. Dichromatism scores are equivalent to  $\Delta S$  (in jnd) calculated from Eq. 2. Assuming a threshold for color discrimination of 1.0 jnd, a large proportion of feather patches sampled (all  $\geq 1.00$  jnd) lie along a continuum of avian sexual dichromatism that is not detectable with human visual capabilities.

feather patch comparison ( $n = 5$  males and 5 females), and larger sample sizes would provide useful information regarding within-sex variance in coloration. If between-sex variances in coloration for many of the feather patches were exceeded by within-sex variances, then the biologically functional relevance (i.e., reliability of plumage color to indicate sex) of intersexual color differences would be in question. Overall, the logistic regression showed small within-sex variances in relation to between-sex variance for many feather patches. Because the goal of this study was to sample widely across taxa, sample sizes were exchanged for taxonomic breadth; nonetheless, my results support the average colors used in the color discrimination model as biologically functional information (29), and a functional correlation between human-invisible coloration and sex for many of the monochromatic<sup>human</sup> species sampled in this study appears clear.

Herein, the visual model calculated distance in avian perceptual color space ( $\Delta S$ ) between each conspecific male and female feather patch. Thus,  $\Delta S$  calculations represent a means to quantify sexual dichromatism (Fig. 3), explicitly considering birds' color discriminatory abilities. Assuming a threshold for discrimination of 1.0 jnd, the magnitude of dichromatism for a feather patch can be calculated as  $\Delta S - 1$ .  $\Delta S$  values for feather patches sampled in this study ranged from 0.06 jnd (head

coloration of *Pseudochelidon eurystomina*) to 12.71 jnd (crown coloration of *Phlegopsis nigromaculatus*); 324 of 552 (58.7%) feather patches sampled would be perceptible as sexually dichromatic to birds ( $\Delta S > 1.0$  jnd; Fig. 3). Although previous research quantifying dichromatism established dichromatism values across species (e.g., refs. 3, 4, and 35), lower bounds for this continuum were set by the limits of human color discrimination. As a result, most studies of sexual selection for elaborate color ornamentation have focused on only a subset of the continuum that is functionally relevant to birds (e.g., many examples in ref. 2). Recent research concluded that avian plumage signals can exploit intertaxon perceptual differences (36), and inclusion of conspecific signals hidden from human investigators but shown in this study to be available to birds could further facilitate understanding of functions of plumage coloration. For example, since the discovery of sexual differences in the blue-UV crown coloration of blue tits (11–12), color in this feather patch has been shown to be important in social interactions (37), mate choice (38), parental care (39), and offspring sex ratios (40).

In conclusion, the Vorobyev–Osorio color discrimination model (19) offers an approach to quantifying sexual dichromatism in relation to avian visual capabilities. My results indicate that sexually monochromatic<sup>avian</sup> passerine bird species are much less common than previously thought. These results have far-reaching implications for behavioral and ecological studies of birds, because plumage signals hidden from human perception might be a pervasive feature of avian coloration and not merely restricted to UV wavelengths. Furthermore, the results of this study refocus questions of plumage evolution toward an explanation of the rarity of monochromatic species, rather than dichromatic species, which could provide novel insights into the role of different selective pressures driving avian plumage evolution.

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- Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex* (Murray, London), 2nd Ed.
- Andersson, M. (1994) *Sexual Selection* (Princeton Univ. Press, Princeton).
- Badyaev, A. V. & Hill, G. E. (2000) *Biol. J. Linn. Soc.* **69**, 153–172.
- Dunn, P. O., Wittingham, L. A. & Pitcher, T. E. (2001) *Evolution* (Lawrence, Kans.) **55**, 161–175.
- Badyaev, A. V. & Hill, G. E. (2003) *Annu. Rev. Ecol. Evol. Syst.* **34**, 27–49.
- Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. S. & Hunt, S. (2000) *Adv. Study Behav.* **29**, 159–215.
- Odeen, A. & Hasted, O. (2003) *Mol. Biol. Evol.* **20**, 855–861.
- Goldsmith, T. H. (1991) in *The Perception of Color, Vision and Visual Dysfunction*, ed. Gouras, P. (Macmillan, London), Vol. 6, pp. 62–89.
- Osorio, D., Miklosi, A. & Gonda, Zs. (1999) *Evol. Ecol.* **13**, 673–689.
- Vorobyev, M. (2003) *Proc. R. Soc. London Ser. B* **270**, 1255–1261.
- Andersson, S., Ornborg, J. & Andersson, M. (1998) *Proc. R. Soc. London Ser. B* **265**, 445–450.
- Hunt, S., Bennett, A. T. D., Cuthill, I. C. & Griffiths, R. (1998) *Proc. R. Soc. London Ser. B* **265**, 451–455.
- Cuthill, I. C., Bennett, A. T. D., Partridge, J. C. & Maier, E. J. (1999) *Am. Nat.* **160**, 183–200.
- Mahler, B. & Kempnaers, B. (2002) *Condor* **104**, 248–254.
- Mennill, D. J., Doucet, S. M., Montgomerie, R. & Ratcliffe, L. M. (2003) *Behav. Ecol. Sociobiol.* **53**, 350–357.
- Mays, H. L., Jr., McGraw, K. J., Ritchison, G., Cooper, S., Rush, V. & Parker, R. S. (2004) *J. Avian Biol.* **35**, 125–134.
- Bleiweiss, R. (2004) *Proc. Natl. Acad. Sci. USA* **101**, 16561–16564.
- Eaton, M. D. & Lanyon, S. M. (2003) *Proc. R. Soc. London Ser. B* **270**, 1721–1726.
- Vorobyev, M. & Osorio, D. (1998) *Proc. R. Soc. London Ser. B* **265**, 351–358.
- Sibley, G. C. & Monroe, B. L., Jr. (1990) *Distribution and Taxonomy of Birds of the World* (Yale Univ. Press, New Haven, CT).
- Vorobyev, M., Osorio, D., Bennett, A. T. D., Marshall, N. J. & Cuthill, I. C. (1998) *J. Comp. Phys. A* **183**, 621–633.
- Vorobyev, M., Brandt, R., Peitsch, D., Laughlin, S. B. & Menzel, R. (2001) *Vision Res.* **41**, 639–653.
- Goldsmith, T. H. & Butler, V. (2003) *J. Comp. Phys. A* **189**, 135–142.
- Hart, N. S., Partridge, J. C., Cuthill, I. C. & Bennett, A. T. D. (2000) *J. Comp. Phys. A* **186**, 375–387.
- Hart, N. S. (2001) *Prog. Retinal Eye Res.* **20**, 675–703.
- Hart, N. S. (2001) *J. Comp. Phys. A* **187**, 685–698.
- Stuart-Fox, D. M., Moussalli, A., Marshall, N. J. & Owens, I. P. F. (2003) *Anim. Behav.* **66**, 541–550.
- Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M. & Summers, K. (2004) *J. Exp. Biol.* **207**, 2471–2485.
- Johnson, D. H. (1999) *J. Wildl. Manage.* **63**, 763–772.
- Barracough, T. G., Harvey, P. H. & Nee, S. (1995) *Proc. R. Soc. London Ser. B* **259**, 211–215.
- Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. (2004) *Proc. Natl. Acad. Sci. USA* **101**, 11040–11045.

32. Omland, K. E. (1997) *Evolution (Lawrence, Kans.)* **51**, 1636–1646.
33. Burkhardt, D. (1989) *J. Comp. Phys. A* **164**, 787–796.
34. Hausmann, F., Arnold, K. E., Marshall, N. J. & Owens, I. P. F. (2003) *Proc. R. Soc. London Ser. B* **270**, 61–67.
35. Owens, I. P. F. & Hartley, I. R. (1998) *Proc. R. Soc. London Ser. B* **265**, 397–407.
36. Hastaad, O., Victorsson, J. & Odeen, A. (2005) *Proc. Natl. Acad. Sci. USA* **102**, 6391–6394.
37. Alonso-Alvarez, C., Doutrelant, C. & Sorci, G. (2004) *Behav. Ecol.* **15**, 805–809.
38. Hunt, S., Cuthill, I. C., Bennett, A. T. D. & Griffiths, R. (1999) *Anim. Behav.* **58**, 809–815.
39. Limbourg, T., Mateman, A. C., Andersson, S. & Lessells, C. M. (2004) *Proc. R. Soc. London Ser. B* **271**, 1903–1908.
40. Griffith, S. C., Ornborg, J., Russell, A. F., Andersson, S. & Sheldon, B. C. (2003) *J. Evol. Biol.* **16**, 1045–1054.